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BREEDING FOR DISEASE RESISTANCE IN WHEAT, OATS, BARLEY AND FLAX[1]

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Bureau of Plant Industry

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INTRODUCTION

Breeding for disease resistance is an important phase of the improvement program with the grain crops, wheat, oats, barley and

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flax, since in these crops diseases cause large losses each year. The underlying principles are similar to those for physiologic and morphologic characters, except that it is necessary to deal with two biologic organisms, the host and the pathogen, both of which are variable and contain heritable factors which condition reaction of the host to the disease organism. This means that the pathogen must receive as intensive study as the crop itself. The ultimate problem in breeding is to combine, in a new variety, resistance to as many diseases as possible together with desirable agronomic characters and quality.

The plant breeder, plant pathologist and cereal chemist, by means of cooperative experiments, have made considerable progress. There are many problems, however, that are yet unsolved. For many diseases, methods and techniques have been developed for creation of epiphytotics, but in other cases, such as root rots, production of uniform epidemic conditions and lack of sufficient resistance in parent stocks have been two of the major limiting factors in breeding for resistance.

Some idea of the importance of growing varieties resistant to various diseases is emphasized by the estimated losses as given in the Plant Disease Reporter for 1935. Estimated losses in the United States for all diseases in wheat, oats and barley were 277 million, 185 million and 53 million bushels, respectively.

DISEASES OF WHEAT, OATS, BARLEY AND FLAX

Wheat, oats, barley and flax are continually subject to ravages of plant parasites. Smuts and rusts are the most obvious and probably the most destructive diseases on wheat and oats, scab is a serious disease on barley and wheat, and wilt and rust are very destructive on flax. Other destructive diseases are the root rots, black chaff, ergot and a number of less common diseases which occasionally also greatly menace production. A complicating factor dealing with most diseases and recognized only rather recently is the presence of races of each organism which, so far as breeding is concerned, is almost the same as breeding for resistance to another disease.

Important diseases of these crops with the most recent published number of physiologic races are given in the following tabulation. These are arranged according to the causal organism. There are

IMPORTANT DISEASES OF WHEAT, OATS, BARLEY AND FLAX

Common Name	Crop	Causal Organism	Number of Physiologic Races	Authority
Black stem rust	Wheat and Barley	*Puccinia graminis tritici* Eriks. and Henn.	177	(134)
Orange leaf rust	Wheat and Barley	*triticina* Eriks.	108	(126)
Yellow stripe rust	Wheat and Barley	*glumarum* (Schu.) Eriks. and Henn.	28	(224)
Stem rust	Oats	*graminis avenae* (Pers.) Eriks. and Henn.	12	(133)
Crown rust	Oats	*coronata avenae* (Pers.) Cda.	45	(162)
Flax rust	Flax	*Melampsora lini* (Pers.) Lev.	24	(84)
Stinking smut	Wheat	*Tilletia tritici* (Bjerk.) and *T. levis* (Kuhn)	24	(124)
Loose smut	Wheat	*Ustilago tritici* (Pers.) Rostr.	4	(160)
Covered smut	Oats	*levis* (K. and S.) Magn.	29	(194)
Covered smut	Barley	*hordei* (Pers.) K. and S.	8	(246)
Loose smut	Barley	*nuda* (Jens.) K. and S.	3	(224)
Loose smut	Barley	*medians* Bied. or *U. nigra* Tapke	2	(245)
Loose smut	Oats	*avenae* (Pers.) Jen.	14	(194)
Stripe disease	Barley	*Helminthosporium graminium* Raph.	20	(46)
Scab	Wheat and Barley	*Gibberella saubinetii* (Mont.) Sacc. or *G. zeae* (Schw.) Petch and *Fusarium* sp.	Many	(79)
Wilt	Flax	*Fusarium lini* Bol.	Numerous	(22)

undoubtedly more physiologic races of many of the pathogenic organisms than are given in the table which have not been reported in the literature.

Dickson (68) has summarized the pathologic descriptions of these and other diseases attacking these crops, giving their life histories and methods of control.

PHYSIOLOGIC SPECIALIZATION AND HYBRIDIZATION OF THE PATHOGEN

One of the difficulties encountered in the early work of breeding for disease resistance was the failure of new productions and varieties to maintain their resistance every year and in all localities. Varieties resistant in one locality or year often were susceptible in another.

Early studies with stem rust, *Puccinia graminis,* showed that it attacks wheat, oats, barley, rye and a number of grasses. Eriksson (80) proved that there are several distinct varieties of rust, as differentiated by the hosts they attack. These rusts could be divided into wheat stem rust and oat stem rust, according to their ability to attack certain hosts of the grass family. *P. graminis tritici* attacks wheat and barley but not rye or oats; the species *avenae* grows only on oats.

Physiologic specialization was first reported in *Colletotrichum lindemuthianum* (Sacc. and Magn.) Bri. and Car. (anthracnose of beans) (78, 16). They found two physiologic strains. Others (223, 228) showed that the two varieties of stem rust were composed of physiologic races that could be distinguished by the manner of reaction when seedlings of a selected group of varieties of wheat, oats or barley were inoculated with collections of rust. Since this discovery, other workers have found physiologic specialization in most all parasitic fungi studied. It has been shown also (223, 227) in stem rust of wheat, *Puccinia graminis tritici,* that these physiologic races are relatively stable and do not often change their reactions to hosts, even when collected from different countries. The Missouri races of loose and covered smuts of oats have been grown annually for more than 20 years and have shown a constant behavior on given varieties of oats (193).

Watson (264) has recently shown that in the seedling stage of wheat the gene for semiresistance to a Brazilian culture of race 15

of stem rust is different from that responsible for resistance to cultures of race 15 from Japan and the United States.

Holton and Rodenhiser (124) found most races of bunt of wheat to be highly stable in tests on winter wheat at Pullman, Wash., although one race, T–11, gave rise to T–13, thus indicating that some races are unstable in pathogenicity.

It has been shown that new races originate by hybridization and mutation. Stakman *et al.* (229) suggested the possibility of stem rust races hybridizing on barberry, and Craigie (64, 65) demonstrated the function of pycnia and aecia in hybridization of the rust fungi. Others (63, 136, 171, 225) have studied a number of crosses and proved that new races of *Puccinia graminis* originate by crossing not only between races but also between varieties. Workers at the University of Minnesota and the Dominion Rust Research Laboratory at Winnipeg, Canada, have reported the F_1 behavior of approximately 14 varietal crosses of stem rust. Only the first generations of these crosses have been studied. They found partial interfertility between varieties in experimental crosses. Also segregates were obtained, some of which had the pathogenic characteristics of one or the other parent variety, others were intermediate for pathogenicity, and finally some were different in pathogenicity from either parent and could be considered as new varieties.

Waterhouse (263) crossed two races of stem rust of wheat and obtained two races previously unknown in Australia. A number of other crosses between races of stem rust have also been studied (137, 171, 172, 225). Interfertility between races is complete. When two races, each homozygous for pathogenicity, are crossed, the F_1 resembles one or the other parent and there appears to be Mendelian dominance. If heterozygous races are crossed, new races which have greater virulence than either parent are obtained sometimes in the F_1. When the F_1 hybrids are selfed, there is evidence of segregation and recombination of factors governing pathogenicity. The parental lines are often recovered, while other races recovered show some of the characteristics of the parents. There is evidence that, in some crosses, certain races are homozygous for pathogenicity, although the majority of them are heterozygous. There is also a tendency toward homozygosity in races of later generations when continued selfing is followed.

Mutation has been reported in all classes of fungi by Christensen

(45), but it does not appear to be of great importance in the evolution of races of stem rusts. However, Stakman *et al.* (225) report that race 1, which had been cultivated and found absolutely stable over 12 years, suddenly gave rise to two new races, 68 and 60, previously unknown. Murphy (163) observed the development of race 33 which apparently mutated from race 1 in *Puccinia coronata.* Mutation certainly is a factor in fungi, other than rusts, where the mutants may differ from their parents in cultural characters, in physiologic characters, in pathogenicity and in morphology.

Races of stem rust of wheat have been inbred by Johnson and Newton (132) who found that certain races produced abnormal characteristics. Most of these abnormal characteristics are detrimental and appear to be governed by recessive factors. If these abnormal races are crossed with a normal race, the abnormalities tend to disappear. Thus, hybridization apparently tends to maintain the normal characters of the race, and it would appear that the chances of abnormal races occurring in nature are rather limited.

There is some indirect evidence of hybridization of the rusts in nature, as most races collected in the field are heterozygous for pathogenicity, which indicates hybrid origin. Stakman *et al.* (226) found a different race of stem rust of wheat for every four isolated from 94 aecial collections from barberries, and a different race for every 1,000 collections from 8,000 uredial collections. There are many races of rust in the Mississippi Valley of the United States and only a few in Australia. Waterhouse (262) suggests that the presence of barberries in the United States and absence of them in Australia probably accounts for this difference, since new races arise in nature through the medium of the barberry. Eradication of the aecial hosts would appear to be important in reducing production of new hybrid races of the rust fungus.

Hybridization of certain smuts has been accomplished with ease under controlled conditions in the laboratory. There is only circumstantial evidence that hybridization occurs in nature (199). There is ample opportunity for hybridization in the field, since mixtures of races and species of organisms having the same life histories are found in the same field, and it is not uncommon to find collections having characteristics common to the two different types, such as *Ustilago avenae* and *U. levis,* the oat smuts, or *Tilletia levis,* or *T. tritici,* bunt of wheat.

Allison (7) found that covered smut of barley, *Ustilago hordei*, hybridized with the loose smut, *U. medians*. Covered smut chlamydospores of the F_1 were echinuate and the head type intermediate. In the F_2, recombinations of head type and wall markings of the chlamydospores were obtained, which differed from either parent. Tapke (247) has shown that *U. medians* is a mixture of the mycelium-producing *U. nuda* and sporidia-producing *U. nigra*. *U. medians* does not exist in the United States or elsewhere and was erroneously based on a mixture of two smuts. Holton (122) crossed a Gothland (C.I.[3] 1898) strain of *U. avenae* with a Monarch (C.I. 1896) strain of *U. levis*. He compared the pathogenicity of the pure lines and hybrid segregates and obtained a new pathogenic strain of *U. levis* which attacks both varieties, Gothland and Monarch. Another new strain of the buff smut fungus which attacks both Gothland and Monarch was produced by crossing the Gothland strain of *U. avenae* with the Monarch buff smut strain, which would not infect Gothland.

Flor (83) showed that hybridization occurs between the two species of smut, *Tilletia levis* and *T. tritici*, as well as between the various races within each of the species. Holton (123) crossed two species of smuts, *Tilletia tritici* (race T–9) and *T. levis* (race L–8). Oro (C.I. 8220) wheat is resistant to T–9 and susceptible to L–8. Hohenheimer (C.I. 11458) is resistant to L–8 and susceptible to T–9. A new pathogenic strain was produced which was less virulent than either parent, yet it attacked both varieties of wheat.

PREVALENCE AND DISTRIBUTION OF RACES

A knowledge of the prevalence and distribution of physiologic races and the use of races of the pathogen common to the region where resistant varieties are to be grown, is basic to a well planned program and will aid the breeder in producing varieties with resistance to all the races prevalent in an area.

In summarizing the epidemiological work on stem rust during the past 10 years, Stakman *et al.* (22) studied the shifts in the populations of physiologic races in the United States. In 1934, race 34 was identified in 22% of the samples collected, while in 1931 it con-

[3] C.I. refers to accession number of the Division of Cereal Crops and Diseases.

stituted only 0.6%. Race 36 constituted 36% in 1934 and none in 1939. In 1930, 0.3% of the samples collected were identified as race 56; 66% in 1938; and 59% in 1939. Their results indicate that temperature and other meteorological factors may be important in these shifts.

Holton and Rodenhiser (125) report five additional races of *Tilletia tritici* and *T. levis* identified from collections made from the principal wheat-growing region. This makes 14 races of *T. tritici* and 10 races of *T. levis* identified from the various collections made in the wheat-growing areas of the United States.

Aamodt (3) has summarized the relation between physiologic races and breeding for disease resistance, and Christensen and Rodenhiser (47) for smut resistance. They (the latter) state that "no other factor has contributed more to the difficulty of obtaining smut-resistant varieties of cereals than physiologic specialization in the pathogenes". Outbreaks of smut on supposedly resistant varieties have been associated, in most instances, with the appearance of previously undescribed races. This has led the plant breeder to test all breeding material to as many physiologic races or collections of the pathogen as are found throughout the area where the variety may be adapted.

TYPES OF RESISTANCE

Comparatively little is known regarding the basis for resistance in relation to many diseases of small grains. Studies, however, have been made on the nature of resistance to stem rust of wheats, and these have been summarized by Stakman and Hart (221), and those to the smuts by Western (267). If the causes of resistance were known in terms of morphology and physiology, it would aid materially in the ultimate solution of the breeding problem. From a plant breeding viewpoint, there are two major types of resistance to stem rust of wheat: physiologic or protoplasmic and adult or mature plant resistance. Stakman (219) showed that resistance to *Puccinia graminis tritici* often is due to incompatibility of the host and pathogen, as evidenced by killing of the host cells by the fungus and the more or less sudden death of the fungus itself. When varieties of plants practically immune from stem rust were inoculated, the fungus gained entrance in a normal manner. However, after the germ tubes enter a host which has protoplasmic resistance, they

kill some of the host cells and then die, so that the fungus is never able to establish itself as an actual parasite. This is known as "protoplasmic" or "physiologic resistance". Protoplasmic resistance functions throughout the life of the plant.

In investigations of stem rust of wheat, it has been found, also, that certain varieties and strains are susceptible to one or more races in the seedling stage, yet are resistant to a collection of races in the adult stage when grown in the field (116). This type of resistance was later called "mature plant" resistance by Goulden *et al.* (98). Two explanations have been given for the mature plant type of resistance. It was proven by Hursch (128) that wheat varieties may be resistant on account of morphologic peculiarities. It is known that rust mycelium develops almost exclusively in the chlorenchymatous collenchyma of wheat stems. The collenchyma bundles are small and separated by schlerenchymatous fibers in some varieties. This makes a very definite limitation to the spread of the rust mycelium. Varieties having a large amount of schlerenchyma and a small amount of chlorenchymatous tissue would be resistant. The amount of schlerenchyma tissue increases as the plants grow older. This may account for the fact that seedlings sometimes appear to be susceptible in the greenhouse, but older plants of the same variety may be resistant in the field.

Hart (104, 105) has amplified and confirmed Hursch's work and found a type of resistance called "functional resistance". She suggested that stomatal behavior of the wheat varieties during early morning hours might be related to rust resistance in the stomata of certain resistant varieties, such as Hope (C.I. 8178) and Webster (C.I. 3480). The stomata of some hybrid derivatives from them remain closed in the morning longer than do the stomata of susceptible varieties.

Peterson (180) studied the stomatal behavior of H–44 (C.I. 8177), Reward (C.I. 8182) and 10 F_4 lines from a cross of H–44 and Reward. Five of the lines were resistant and five were susceptible. He found no correlation between stomatal behavior and mature plant resistance. In a study of resistant and susceptible F_2 plants from a cross of Renfrew (C.I. 8194) and H–44, similar results were obtained. He concluded that the main resistance of H–44 is not due to stomatal behavior. Ausemus (12) made a similar study in a triangular cross of Hope, Marquillo (C.I. 6887) and

Supreme (C.I. 8026). Four resistant and four susceptible lines of each of the three crosses and the parents were studied in the field. No correlation was found between stomatal behavior and rust reaction.

Stakman and Hart (221) concluded that there are at least three well defined types of resistance of wheats to *Puccinia graminis tritici*. A variety may possess one, all or a combination of these types. The more types of resistance it has, the more likely it will be to resist rust in the field. All known varieties have rust more or less heavily under certain conditions. All these types of resistance are subject to considerable variation, just the same as other plant characters. The degree of this variation and the frequency of its occurrence under a reasonable normal range of conditions will determine when and to what extent a variety will be resistant.

Western (267) concluded that resistance to smuts may be physiologic, morphologic, functional or due to interaction of all three types. Various degrees of resistance to smuts were found. Almost all collections of *Ustilago avénae* and *U. levis* were able to penetrate into the coleoptile of susceptible and resistant varieties. In some cases the mycelium entered the tissues of the coleoptile, but its development was very slight and accompanied by marked necrosis of the host cells, resulting in death of the pathogen. This type of necrosis suggests a condition similar to that in certain hypersensitive wheats when attacked by stem rust (219, 6), but it is not sufficiently general in occurrence to conclude that hypersensitiveness alone may express the phenomenon of smut resistance in oats. In slightly less resistant varieties the mycelium persists for a much longer time with only slight necrosis of the host cells. Less resistance is shown by those varieties in which the mycelium persists for a considerable period but fails to reach the young meristematic tissues of the growing points of the plants. Similar observations were made by Kolk (144) in *U. avenae*, and Woolman (269) has found similar degrees of resistance in wheat to infection by bunt.

Peatland (C.I. 5267) barley is very resistant to loose smut under natural conditions. However, Moore found this variety heavily infected when inoculated by the partial vacuum method (161). Similar results were obtained by Christensen and Powers (unpublished data) when the heads were exposed and the glumes clipped. Peatland's resistance lies apparently in the location of the heads in the

boot during the susceptible period, where the smut spores do not readily reach them. This has been called morphologic resistance. Western (267) found that at least two races of *Ustilago avenae* were unable to penetrate into the cells of Markton oats. Whenever germ tubes attempted to enter, a pad of sufficient thickness to prevent their entrance was formed. Other races were able to penetrate both resistant and susceptible varieties.

The relation of host vigor to smut infection has been studied. It was early observed by Brefeld (23) that rapidly developing seedlings of oats and sorghums produced fewer smutted plants than did comparable series in which growth was slower immediately following germination. Western (267) suggested this was functional resistance. Faris (81), however, failed to find a significant correlation between the vigor of wheat plants as affected by fertilizers and infection by bunt, but concludes that conditions favorable for growth of the plant are also favorable for growth of the pathogen. Noble (175) obtained greater percentages of smut by cutting back rye and oats. In contrast to this, Reed and Faris (195), working with smuts of oats and sorghum, and Tapke (243), working with loose smut of wheat, did not find any correlation between speed of germination, or host vigor, and smut infection.

Heald and Gaines (117) reported Hope, a spring wheat, to be susceptible to bunt when planted in the fall, but resistant when planted in the spring. Smith (214) found that Hope was relatively resistant when grown at relatively low temperatures until emergence from the soil and then grown under high temperatures, although plants grown continuously in cool environment were susceptible. He concluded, however, that the Hope resistance is not due to more rapid development of the plant at the higher temperature, but is dependent upon either nutritional conditions or an organization of the protoplasm that at the higher temperature retards or inhibits growth of the fungus.

The effect of environment upon interaction of host and pathogen also may be important. For example, Hope wheat, which had the mature plant type of resistance and has proven highly resistant to all races of stem rust in the United States and Canada, was found to be susceptible when grown by Abbott (5) in Peru. Whether this difference in reaction is due to environment or to physiologic races has not been determined. Hart and Zeleski (106) and John-

son and Newton (135) found that under reduced light intensity Hope became more susceptible to race 21. High temperatures (26° to 33° C.) (106) tended to increase resistance of the plants. Johnson and Newton (135), on the other hand, found a constant high temperature (75° to 80° F.) capable of causing partial or even complete breakdown of the mature plant resistance of Hope. Reduction in the length of daily light period also influenced the rust reaction of the plants toward susceptibility (135).

Other varieties—McMurachy (C.I. 11876), Eureka, R.L. No. 1534, and several Kenya wheat strains from Kenya, East Africa—which appear to have the physiologic type of resistance, were immune from stem rust under normal conditions. They lost their characteristic reactions when grown under constant high temperatures (173). The reaction tended to moderate resistance or even susceptibility. Iumillo (C.I. 1736), a wheat almost immune to stem rust, showed occasionally a tendency toward moderate resistance. Since inheritance of a character is the manner of reaction of the genes under certain environmental conditions, this "breakdown" of immunity or resistance may occur in regions when temperatures are excessively high for considerable periods.

Environment often affects development of the pathogen. Melander (158) has shown that development of stem rust of wheat is almost suppressed at 0° to 1° C., although the capacity for normal rust development is generally recovered on exposure of the infected plants to 10° to 20° C. The optimum temperature for stem rust development is 20° C. Johnson and Newton (131) found that for temperatures above the optimum for rust development, the higher the temperature the less vigorous the pustule development. For example, moderately high temperatures (about 75° F.) favor maximum pustule development of certain physiologic races of stem rust of wheat and oats and crown rust of oats (94, 130, 183, 262), while temperatures below 60° F. tend to inhibit pustule development (in certain physiologic races) on some host varieties. Leaf rust of wheat and crown rust of oats are less tolerant of high temperature than is stem rust of wheat. Physiologic races of the same rust differ in their sensitiveness to temperature.

BREEDING FOR DISEASE RESISTANCE STUDIES

Stem rust of wheat. Considerable progress has been made in the development of crop varieties resistant to various rusts, and much

information has been accumulated regarding inheritance of rust reaction. In addition to the breeding program, eradication of the alternating host, to prevent hybridization of the parasite, is of value in a long-time improvement program. During the early years of breeding for resistance to stem rust it was observed that Einkorn, some of the durums, spelts and emmers were the only wheats that were highly resistant to stem rust (43). Crosses of the emmers and durums with susceptible common wheats involved sterility and linkage between rust resistance and the undesirable durum and emmer characters. Hayes *et al.* (114) found resistance partially dominant in crosses of *Triticum vulgare* with *dicoccum*. There was an apparent linkage of rust resistance and emmer type of plant. However, some rust-resistant, vulgare-like F_2 plants were obtained. In crosses of *vulgare* with *durum*, susceptibility was dominant, and a strong linkage was observed between rust resistance and the durum characters. From the cross of Iumillo, a resistant durum, and Marquis (C.I. 3641), the new variety Marquillo (a vulgare wheat) was produced which was resistant to a collection of races in the field. Others (96, 103, 182, 248) have also succeeded in combining the resistance of durum or emmer varieties with *vulgare* characters.

The discovery of physiologic races suggested the need of determining the mode of inheritance of the reaction to individual races. Puttick (188) studied the reaction of the F_2 generation of a Mindum (C.I. 5296) × Marquis cross to rust races 19 and 1 in the greenhouse. Mindum was susceptible to race 19 and Marquis resistant, while to race 1 the reaction was the reverse. From this cross he obtained plants which were resistant to both races. In further studies on the genetics of rust resistance in wheat, Aamodt (1, 2), in a Kanred (C.I. 5146) × Marquis cross, showed that one genetic factor governed the immunity in Kanred to 16 races. A similar relationship was found in a H–44 × Marquis cross by Goulden *et al.* (98), in which one factor controlled the reaction to six different races. Neatby (168) studied the seedling reaction of 15 races in a cross of H–44 × Marquis and found the races fell into three groups of seven, five and three. Two sets of factors were identified, one which affects the reactions to races of groups I and II, and another which affects the reactions to groups I and III. He concluded that each of the two sets of factors consisted of only one pair.

Several new wheats have been discovered recently in the Kenya Colony of Africa which are resistant to all prevalent races in Aus-

tralia (149). Some of these wheats have been resistant to 20 physiologic races (181) and were resistant in the mature plant stage in the field to 30 prevalent Canadian races.

Physiologic races in stem rust are differentiated on the basis of seedling reaction. Studies have been made between seedling reaction in the greenhouse and field reaction. Several workers (98, 102, 109, 116, 168) have found that the mature plant reaction to a collection of races of stem rust in the field may be inherited independently of the seedling reaction to a known race or races in the greenhouse.

Kota (C.I. 5878), a common hard, red, spring wheat, was found (261) to possess some resistance to stem rust in the field, although this resistance was not sufficient to guard against all loss. In crosses where Kota or Iumillo, a durum, were the resistant parents, resistance was found to be recessive in the F_1. In the F_2 the inheritance of the rust reaction was rather complicated, often none of the plants being as resistant as the resistant parents.

Hayes *et al.* (116) crossed a sister selection of Marquillo (which is resistant to a collection of physiologic races in the field) with a Kanred × Marquis selection which had the Kanred immunity to 11 races in the seedling stage, and concluded that the factors for resistance of the Marquis × Iumillo parent in the field were inherited independently from the factor for immunity from certain races in the seedling stage. The field reaction was controlled by two main factors with possibly modifying factors. Thatcher (C.I. 10003) was produced from this cross.

McFadden (155, 156), from a cross of Yaroslav (C.I. 1526) emmer and Marquis, obtained Hope and H–44, both of which are varieties of the common wheat type and very highly resistant under field conditions, not only to stem rust, but also to leaf rust, bunt and loose smut. They are susceptible to black Chaff, *Phytomonas translucens* var. *undulosum* (Sm. J. and R.).

These two wheats were made available to many plant breeders, and Goulden *et al.* (97, 98) were the first to report on the results of crosses with H–44 as one parent. In crosses between H–44 and Marquis they found that under conditions of an epidemic created by seven physiologic races, field resistance was controlled by a single pair of factors.

The first studies on inheritance of field resistance, using Hope as

the resistant parent, was reported by Clark and Ausemus (56, 57). They found that resistance of Hope in crosses of Hope × Marquis or Reliance (C.I. 7370) (two susceptible varieties) was inherited as a dominant character, as shown in F_1 and F_2, and further results based on F_3 data were explained on a two factor basis. In a Hope × Ceres (C.I. 6900) cross only a single factor difference was shown. This dominance was a new character in common wheats. No sterility is involved in crosses of the Hope and H–44 wheats with other common wheats, and a large number of nearly rust-free plants and strains was obtained from hybrid populations.

Neatby and Goulden (169) found two complementary factors governing field resistance in a Marquis × Hope cross and at least two pairs of factors for resistance in a Reward × Hope cross, while Reward carried an inhibitor for the resistance of Hope.

Quisenberry (189), working with a cross H–44 × Minhardi (C.I. 5149), found that in F_2 a single factor difference for susceptibility and resistance in the field was indicated. When F_3 lines were tested, the single factor hypothesis seemed inadequate.

Crosses between the varieties Marquillo, Hope and Supreme were studied by Ausemus (12). In the Hope × Marquillo cross the Marquillo type of resistance was inherited in a very complex manner. Moreover, in this cross, involving a resistant and semiresistant parent, F_3 lines that were more susceptible than either parent were obtained. It was concluded that the factors for resistance and semiresistance in these varieties were not allelomorphic. Sixty-seven segregating F_3 lines were classified for the total number of resistant plants and for the combined total of semiresistant and susceptible plants. Fifty families segregated in a 1:3 ratio, eight in a 1:15 ratio, and nine in a 9:7 ratio. It was believed that three or more factors were concerned in the inheritance of rust reaction in this cross. Hayes *et al.* (11), in crosses of H–44 with the moderately resistant Double Cross and a Kota × Marquis selection, concluded that the inheritance of the mature plant reaction of H–44 was dependent on a single factor pair. The moderate plant resistance of the Double Cross and Kota × Marquis selections appeared to be dependent on factors not allelomorphic to the factors controlling the mature plant resistance of H–44. The inheritance of reaction to stem rust and bunt, leaf rust and bunt, leaf rust and black chaff, and black chaff and bunt appeared to be independent, as determined

by the χ^2 test. There appeared to be a linkage in inheritance of reaction to stem rust and leaf rust and of reaction to stem rust and black chaff.

Kulkarni (147) studied a cross of Hope with Liguleless (a very susceptible variety) and obtained a ratio of 13 susceptible to 3 resistant plants in the F_2 and F_3 generations. He concluded that Hope carried a dominant factor for resistance and Liguleless had a dominant inhibiting factor I, which in the presence of Hope resistance factor gave susceptibility. A resistant (Ceres × Hope) parent was crossed with a semiresistant (Ceres × Double Cross) parent and showed that the Ceres × Hope parent had two factors—A for resistance and B for semiresistance—while the other parent had the genotype aaBB. The segregation of a random F_3 of the latter cross indicated that the Hope type of resistance in the field to a collection of races was differentiated by a single factor pair. Clark and Humphrey (58) and Clark and Smith (61), in studies of inheritance of reaction to stem rust in three crosses—H–44 × Ceres, Hope × Reliance, Hope × Marquis—concluded that H–44 and Hope have two major dominant factors controlling resistance. In crosses of Hope and H–44 with the more susceptible varieties, Supreme, Power and Reward, Clark (53) found inheritance to be more complicated. Data from these crosses indicate that there is more than one factor for susceptibility and that these factors may differ in amount of effect. They report that there is little evidence of more than one dominant factor for the high type of resistance of the Hope and H–44 type, as segregation for rust reaction is usually definite. Clark and Smith (61) were unable to show any minor or modifying factors operating in the three above-mentioned crosses. It appears, however, there must be modifying factors, since it is difficult to obtain strains with as complete freedom from rust as in the Hope and H–44 parents.

Churchward (50) concluded that at least two major factors and some modifiers controlled field resistance to race 34 in a Hope × Federation (C.I. 4734) cross, although there was a rather wide variation in the ratios of resistant to susceptible plants.

Pan (177) crossed two resistant parents (Marquis × H–44 and Pentad × Marquis) with other resistant parents (Double Cross, Hope and H–44) and studied the inheritance of mature plant reaction to a collection of races of rust in the field. Double Cross

appeared to have two complementary factors for semiresistance. When Double Cross was crossed with Pentad (C.I. 3322) × Marquis, most of the hybrids were semiresistant, so it was concluded that these parents had the same genetic constitution. Marquis × H–44 was crossed with Hope and H–44, and all the plants were resistant, showing the genetic factor for resistance in the Marquis × H–44 parent was allelic to that carried by Hope and H–44. This shows indirectly that the genetic factor for resistance in Hope was allelic to the one for resistance in H–44.

Many of the resistant derivations obtained from crosses of H–44 and Hope with other common wheats tend to be susceptible to heat and drought injuries and to diseases causing blackening of stems and glumes. Because of these difficulties, other crosses have been made with Iumillo as a source of resistance to stem rust. Peterson and Love (182) obtained evidence which indicated that mature plant resistance of one of the *vulgare*-like lines of the Iumillo-*vulgare* cross is more simply inherited than that of Iumillo when crossed with other *vulgare* wheats. The inheritance appears to be more complex than that of the Hope or H–44 in the intra-*vulgare* crosses.

In durum crosses of Iumillo with Mindum, Waddell (258) found some correlation between the seedling reaction to race 21 in the greenhouse and the reaction of the mature plants in the field. Some families were resistant in both the seedling and mature-plant stages, some susceptible in both stages, and some susceptible in the seedling but resistant in the mature stage. It was possible to select lines resistant in the mature stage on the basis of their reaction in the seedling stage to race 21. It appears, then, that Iumillo carries a factor for mature plant resistance as well as a factor for physiologic resistance. The results of this study indicate that simple and inexpensive greenhouse tests with seedlings and with but one physiologic race may be used to eliminate some lines that will be in the field in durum crosses involving Iumillo. Types with mature plant resistance would be discarded by use of this method.

Peterson *et al.* (181) tested a series of Kenya wheats and the McMurachy variety and found them resistant to all races to which they were tested in both the seedling and mature stages in the field. Where reaction to both stages was controlled by the same factor, the breeding problem was further simplified.

Watson (264) found that stem-rust resistance in the field was simply inherited when two rust-resistant varieties, Kenya 744 and Kenya 745, were crossed with two susceptible varieties. The genetic factors controlling seedling reaction of Kenya 744 and Kenya 745 were inherited independently when these two varieties were crossed. Further study showed that seedling reaction of Kenya 745 to certain races is controlled by one factor, while seedling resistance to another group of races is governed by two independent factors, one of which causes resistance to races in the first group. He concludes that Kenya 745 may have several factors for rust resistance. Watson stated: "the resistance of Kenya 745 in the field was inherited simply because only a few races of rust developed to epidemic proportions in a rust breeding nursery".

Macindoe (149) crossed several resistant Australian wheats with susceptible varieties and found the field reaction to a large number of races in the United States to depend on a single factor pair difference. Where resistant parents, such as Kenya-Gular, Gaza × $Bobin_2$ and Egypt Na, exhibited physiologic resistance to race 34, the prevailing race in Australia, there was a close association between the seedling reaction to this race and the field reaction to a group of races. In most cases inheritance was relatively simple and apparently controlled by the same factor or factors.

Many crosses studied in recent years involve Hope or H–44 varieties which were selected from a cross of Yaroslav emmer, *Triticum dicoccum,* with Marquis. When these wheats are crossed with other *vulgare* varieties, segregation for stem rust in the F_2 may be normal, but abnormal segregation occurs in some of the F_3 lines. Such were found by Ausemus (12) in the Hope × Marquillo cross. Fifty families segregated in the F_3 in ratio of 1:3, eight in a 1:15 ratio, and nine in a 9:7 ratio. Churchward (50) found similar deviations in a Hope × Federation cross. Ausemus (12) pointed out that these abnormal ratios may be due to abnormal chromosomal behavior of the Marquillo, as found by Powers (185), or of H–44, as found later by Myers and Powers (166). Hope and H–44 are derivatives of a species cross and may also exhibit variability in chromosomal behavior. The tendency for a modified type of segregation in F_3 in some families may make it more difficult to select desirable homozygous types and requires greater care in selecting to make sure the new selections are true breeding.

Triticum timopheevi (C.I. 11802), a dicoccum wheat, was recently introduced into the United States. This variety is reported (69) to be highly resistant to the rusts, *Puccinia triticina* and *P. graminis tritici,* and to powdery mildew (*Erysiphe graminis*) (March.). When *T. timopheevi* was crossed with *vulgare* wheats, several unsuccessful or sterile crosses were recorded by Pridham (187). Jukubziner (187) claimed to have a successful cross between the two species but failed to recover the resistance of the *T. timopheevi* parent. Dickson and Shands (69) obtained fertile hybrids when this species was crossed with common varieties, and the F_1 generations were intermediate or susceptible to *P. triticina.* Sando, as reported by Clark (53), obtained a small percentage of seeds by backcrossing to the common wheat parent.

Pridham (187) crossed *Triticum timopheevi* with Steinwedel (C.I. 5126) (a *vulgare* wheat). Steinwedel was used because of the fertility obtained when it was crossed with the 14-chromosome wheat, Khapli emmer (C.I. 4013), as reported by Waterhouse. Several selections from the F_5 generation were immune to both leaf and stem rusts in Australia, and some of the wheats are of fair agronomic type and appear to be *vulgare* wheats.

Kostoff (145) reported that the F_1 of *Triticum timopheevi* × *T. monococcum* was crossed with a 28-chromosome durotugidoid segregate from the F_4 of the cross *T. turgidum–dicoccum–vulgare.* One of the resulting plants was morphologically identical with the F_1 but had 42 chromosomes and was fertile, having evidently arisen from an unreduced egg cell. This hybrid was thought to be of practical value, in that, having 42 chromosomes, it might be crossed with *T. vulgare* and so introduce the disease resistance of *T. timopheevi* into this species.

It is difficult to transfer the high degree of resistance to fungus diseases characteristic of the species *Triticum timopheevi* and *T. monococcum* to *T. vulgare,* since the hybrids are usually self-sterile. Kostoff (146) produced the amphidiploid *T. timococcum* ($2n = 42$) by crossing *T. timopheevi* with *T. monococcum.* *T. timococcum* has proven completely immune from all fungus diseases. Kostoff suggests this wheat should be very promising material for breeding purposes.

Triticum timopheevi was crossed with a number of varieties of *T. vulgare* by Shands (211). In one cross, *T. timopheevi* × Ill.

I–Chinese was backcrossed to Wisconsin Pedigree No. 2 (C.I. 6683). From the progeny of one fertile plant, several lines have been isolated in the F_6 which are resistant to either leaf or stem rust and a small number are resistant to both rusts, and are of the *vulgare* type.

Wheat-rye hybrids, which were low in yield but very winter hardy, good in milling and baking qualities, and resistant to both rusts and mildew, have been reported by Rosensteil (201). Tzitzen (256) crossed certain species of *Agropyron* and claims to have obtained 183 constant forms which are annuals. Most of them are said to be equal to the standard wheat varieties in yield, some are superior and better in grain quality. Some are immune from bunt, others from rust.

Three types of inherited reactions now known, as pointed out by Clark (51), are near immune, resistant and susceptible. Crosses with the new species, *T. timopheevi,* or with rye or the agropyrons may add new factors for resistance. Combining the resistance factor now known with factors for resistance from these new species may be necessary to insure freedom from rust injury under any environment.

Stem rust of barley. Powers and Hines (186) reported that the mature plant resistance to stem rust, *Puccinia graminis tritici,* of Peatland was inherited as a simple dominant in crosses with susceptible varieties. Reid (197) also found a single factor pair controlling stem rust reaction in the field in a cross of Barbless (C.I. 5105) and Peatland. Shands (210) observed that Chevron (C.I. 1111) was resistant to stem rust in a number of localities. In backcrosses with Chevron as the resistant parent and Barbless (Pedigree 38), Velvet (C.I. 4252) and two other smooth-awned hybrid selections as the susceptible recurring parents and other crosses involving the Chevron parent with susceptible parents, he found that reaction to stem rust was dependent on a single factor pair difference.

Brookins (38) reported results similar to those of Powers and Hines (186) and Reid (197) and that the factor pair controlling rust reaction in Peatland was linked with the factor pairs F_c f_c and Br br located in the seventh linkage group. The F_3 lines reacted to single races 19, 36 and 56 in the seedling stage in a manner similar to that of a large collection of races in the mature plant

stage in the field. It would appear that Peatland has the physiologic type of resistance, since a single factor pair controlled rust resistance both in the seedling stage and in the field.

Peatland and Chevron are now being used extensively in breeding new varieties resistant to stem rust.

Stem rust of oats. Stem rust resistance in oats is inherited as a dominant character, and various investigators (91, 112, 113, 212, 255) report segregation in various crosses studied on a single factor-pair basis. Dietz (70, 71) found a similar explanation of inheritance in certain crosses, but in one cross he obtained a ratio of 3 resistant to 13 susceptible. Welsh (265) studied a number of crosses and found the resistance of Hajira (C.I. 1001) to races 1, 2, 3, 5 and 7 to be governed by the same genetic factor. In another cross of Joanette (C.I. 1880), resistant to race 4 was crossed with Hajira. He obtained a ratio of 9 resistant to 7 susceptible. Gordon and Walsh (95) found resistance to race 4 to be inherited independently of resistance to races 1, 2, 3, 5 and 7, and to depend on a single factor difference in a Hajira-Joanette cross. In five other crosses of resistant and susceptible varieties, resistance was dominant and depended on a single factor pair. Welsh (266) obtained transgressive segregation to race 6 in a cross of Hajira × Joanette.

Smith (212) concluded that a series of three allels controlled stem rust reaction to five physiologic races, 1, 2, 3, 5 and 7, one governing resistance to all five forms; another resistance to 1, 2 and 5, and perhaps 8 and 9, and susceptibility to 3 and 7; and another susceptibility to all five races. Rainbow (C.I. 2345) is resistant to all five races, while Green Russian (C.I. 2890) is resistant to races 1, 2 and 5, but susceptible to races 3 and 7. However, if reaction to all races were controlled by a single series of allelic factors at the same locus on a single pair of chromosomes, it would be impossible to combine factors controlling resistance to different races into a single homozygous individual. In oats there is good agreement between seedling reaction to one or more physiologic races in the greenhouse and the mature plant reaction to a collection of races in the field.

Varieties of oats are available which are resistant to several of the common races of stem rust. Crosses have been made with varieties having otherwise desirable characters, and resistant varie-

ties have been obtained which protect these varieties from serious injury in most years.

Stripe rust of wheat and barley. Stripe rust causes severe losses in areas where conditions favor its development. Biffin (18) found that the host reaction to stripe rust, *Puccinia glumarum,* was inherited as a simple Mendelian character. Susceptibility was dominant over resistance, and in F_2 ratios of 3 susceptible to 1 resistant were obtained. He concluded that rust reaction was inherited independently of any morphological characters. He (20) was able to combine resistance to stripe rust with desirable agronomic characters. Nilsson-Ehle (174), in a cross of resistant × susceptible, was unable to explain his results on a single factor difference. Armstrong (9) obtained results similar to those of Biffin in a cross of immune × susceptible varieties.

Bever (17) studied the varietal reaction to stripe rust of 317 American wheat varieties, including common, club, durum, emmer, poulard and polonicum wheats, and 1,284 foreign introductions. He found, in general, that the common white group was more susceptible than either the soft red winter, hard red winter or durum. The durum group was the most resistant of any. The club wheats, as a group, were the most susceptible, there being only one resistant variety in the entire group.

Straib (241) studied the mature plant reaction of five *Triticum vulgare* crosses in the field. Susceptibility was dominant and the results were complicated, except in two cases where ratios of 3 susceptible to 1 resistant were obtained in the F_2. Many commercial varieties are resistant.

Puccinia glumarum also attacks barley. Straib (240) tested 508 varieties of barley to dwarf rust, *P. simplex* (Korn) Eriks. and Henn., and found a few varieties which were resistant. These varieties were also resistant to stripe rust or *P. glumarum.* In studies of 11 crosses, Straib (242) found the reaction in the F_3 generation to certain races of yellow stripe rust to be dependent on one or two genetic factors, depending on the cross involved.

Leaf rust of wheat. Many studies (*e.g.,* 42, 152, 159) have resulted in finding a number of varieties of wheat resistant to leaf rust. Mains *et al.* (153), in crosses using Kanred and Malakoff (C.I. 4898) as the resistant parents and a susceptible variety as the other parent, found the resistance of Kanred in the field to

depend on several factors. In crosses with Malakoff it was impossible to determine the number of genetic factors involved. After studying a number of crosses they concluded that resistance to various physiologic races of leaf rust was due to different factors or groups of factors inherited as a unit, the different factors of groups being independently inherited.

Hayes *et al.* (110) studied progenies of H–44, a leaf rust-resistant variety crossed with two susceptible varieties. It was easy to recover the type of leaf rust resistance of H–44 parent, and while it was impossible to determine the number of genetic factors involved, it appeared that only one or two factor pairs were necessary to explain the results obtained.

Leaf rust of barley. Waterhouse (262) was apparently the first to report a study of inheritance of resistance to leaf rust of barley. One hundred nineteen varieties of barley belonging to 16 species were tested in the greenhouse to one Australian physiologic race. Sixteen showed resistance. They belonged to *Hordeum vulgare* and *H. distichon.* Certain crosses of these resistant varieties were made with commercial varieties, and in the F_1 resistance was completely dominant. In later generations segregation was a ratio of 3 resistant plants to 1 susceptible. The results indicated a correlation between reaction to *Helminthosporium sativum* P. K. and B. and leaf rust.

Mains and Martini (154) tested a large number of barley varieties in the greenhouse for their reaction to leaf rust. Resistant varieties were found scattered throughout most of the barley groups. Two physiologic races, 1 and 2, were used. Some varieties were resistant to one race but susceptible to the other, while a number of them showed marked resistance to both races. Varieties differed considerably in their reaction in the greenhouse and in the field. Some strains of Horsford (C.I. 877), when inoculated in the seedling stage in the greenhouse with physiologic race 1, were more resistant than when infected with the same race in the field in the heading stage. On the other hand, some varieties were more resistant in the field than in the greenhouse. There was no correlation between leaf rust resistance and mildew resistance.

Johnston (138) studied the seedling reaction of certain cultivated varieties and wild species of barley to physiologic races of leaf rust of wheat. None of the varieties proved to be fully susceptible.

Greater differences in response to wheat leaf rust were observed when several varieties were inoculated with a single race than when one variety was inoculated with several different physiologic races.

The largest number of varieties and species exhibiting pustule formation occurred in the 14 and 28 chromosome groups. *Hordeum nodosum,* which Griffee (101) found had 42 chromosomes, was highly resistant. This is the reverse of conditions in the genus *Triticum* where the largest number of resistant varieties falls in the species having the lower chromosome number, and most of the highly susceptible varieties occur in the *vulgare* group having 42 somatic chromosomes.

Crown rust of oats. Early workers (77, 148, 178) found that certain varieties had considerable resistance to crown rust. Murphy (163) observed that varieties resistant in the seedling stage were also resistant in the adult stage, no varieties being more susceptible as adult plants than as seedlings. Varieties susceptible as seedlings, however, were not always susceptible as adults.

Parker (179) studied seedling reaction of resistant × susceptible varieties and concluded that susceptibility was partially dominant and that multiple factors controlled the reaction. In other crosses of the same type, using different varieties, resistance was found (67, 73) to be partially dominant and the F_2 segregation to be 3 resistant to 1 susceptible. Dietz and Murphy (73), in another cross, found susceptibility dominant and segregation to be controlled by two factor pairs.

Until introduction of Victoria (C.I. 2401) from South America and of Bond (C.I. 2733) from Australia, which are resistant to many races of crown rust (236), there were no varieties highly resistant to crown rust. Using Victoria, a variety highly resistant to a number of physiologic races of crown rust, as the resistant parent in crosses with susceptible varieties, Smith (212) found that more than a single factor was involved in inheritance of the reaction. In one cross studied, crown-rust resistance was associated to some extent with lateness of maturity.

Stanton (231) noted that Matsura (1931) in a genic analysis of *avena* species and varieties reported that a single factor pair controlled crown rust reaction.

Hayes *et al.* (113) and Torrie (255) crossed Bond, a variety highly resistant to crown rust, with susceptible varieties and found

resistance or semiresistance to be dominant. In one cross Hayes *et al.* (113) obtained a ratio of 3 resistant to 1 susceptible, indicating a single factor pair difference, while other crosses gave a segregation of 9:7, indicating two major factors controlling reaction to crown rust. Torrie (255), in an Iowa 444 (C.I. 2331) × Bond cross, found indications of two types of factors: "S", a factor for crown rust resistance, and "I", a factor which partly inhibits expression of "S". The masking effect of the inhibitor on the factor "S" was found to be greater in the mature plant stage in the field than in the seedling stage in the greenhouse. The F_1 seedling reaction indicated partial dominance of resistance, while the mature plant reaction in the field showed partial dominance of susceptibility. In general, there was close agreement in both studies between seedling and mature plant reactions to crown rust. Segregation obtained in the seedling stage to individual races of crown rust was essentially similar to that secured where composite inoculum was used.

Flax rust. In 1926 Henry (119) reported that several previous investigators had observed differential rust reaction in different varieties of flax, some reporting immune varieties or types. Later in his work at Minnesota he (120) found the varieties Ottawa 770B (C.I. 355), Argentine (C.I. 271) and Bombay (C.I. 42) to be immune from a number of collections of rust from the United States, Canada and the Netherlands. In several crosses, in which one of the parents was immune, he (119) found immunity dominant in the F_1, and a segregation of either 3:1 or 15:1 in the F_2 generation. An immune Argentine selection was crossed with Saginaw (C.I. 207) and immunity was dominant in the F_1, with the F_2 generation segregating 15 immune to 1 susceptible. In other crosses he found immunity of Ottawa 770B and Bombay in each case to be dependent on a single dominant factor pair. This makes the problem of breeding for rust resistance relatively simple.

Myers (165) studied the nature of genes conditioning the same type of reaction to rust and the relationship of these genes in different varieties with one race and to a collection of races of rust. Thirty-seven crosses involving 17 strains and varieties of flax were used.

In the field and in greenhouse studies where a collection of rust races were used, certain parent varieties were found to be immune,

resistant, semiresistant and moderately susceptible. In crosses involving parents with the various types of rust reaction, immunity was dominant over near immunity; resistance, susceptibility and resistance were dominant over semiresistance and susceptibility. The reaction to a collection of rust races in crosses involving Ottawa 770B, Newland, C.I. 438, C.I. 416–3 and C.I. 712 was explained by assuming factors in two different allelic series, L and M. L and M are duplicate factors conditioning immunity, and l^n and m^n condition near immunity, l^n being allelic to L and m^n allelic to M. The genotype of Ottawa 770B was LLmm; Newland, llMM; C.I. 438, LL $m^t m^t$; C.I. 416–3, ll $m^n m^n$; and C.I. 712, $l^t l^t$mm.

A single major factor apparently conditioned resistance both in Light Mauve (C.I. 379–1) and in Bolley Golden. Crosses with Ottawa 770B indicated that neither of these varieties carried a factor for resistance allelic with L.

The immune strain of Bolley Golden (C.I. 644) carried two factors conditioning immunity and resistance, respectively, to the collection, while a single major dominant factor conditioned the near immunity of the variety of Light Mauve.

In general, the reaction of hybrids to race 4 was similar to their reaction to the collection of rust.

Bunt or covered smut of wheat. Farrer (82) reported attempts to breed wheats in Australia for resistance to bunt, or stinking smut, *Tilletia tritici* or *T. levis,* by hybridization. After his death in 1906, Florence and Genoa, two highly resistant varieties, resulted from his crosses.

Gaines began his work with bunt in 1915, and in 1923 (86) reported extensive investigations. The varieties and hybrids were grouped into four classes, susceptible, intermediate, resistant and "immune". When resistant varieties were crossed with susceptible ones, susceptibility was dominant. When susceptible were crossed with "immune" varieties, Martin (C.I. 4463) and Hussar (C.I. 4843) (87), resistance seemed to be dominant. His results indicated that immunity or resistance is due to the combined effect of several factors. When all factors are present, as in immune varieties, they produce apparent dominance, but a lesser number gives the recessive effect.

Briggs (24, 26–33) found three different factors for bunt resistance; the one in the Martin variety of wheat was dominant. The

Hussar and Turkey (C.I. 1558) factors for resistance were somewhat intermediate in that bunt developed in about half of the heterozygous plants. In a large number of crosses he has shown the inheritance of bunt reaction to be relatively simple, depending on one or two factors. He worked principally with one race of bunt to which Martin and Hussar are resistant.

Clark *et al.* (60), in crosses between Hope and less resistant varieties, found that several factors were involved, but the greater the resistance in the parents, the less complicated was the inheritance. Aamodt (2) concluded that multiple factors controlled bunt in crosses studied by him. Hayes *et al.* (110) and Ausemus (12) were unable to determine the number of factors responsible for bunt reaction in certain crosses having H–44 or Hope as one of the parents. Smith (213) and Clark (53) report that Florell and Bayles have transferred the immune reaction of Hussar into new hard red spring wheats. Clark (51) found that two selections developed by Smith (213) and Florell and Bayles, when crossed with susceptible varieties, produced bunt-free plants in the F_1, thus showing dominance of the near immune reaction. Clark and Rodenhiser, according to Clark (53), found these crosses to show a single factor segregation in the F_2 and F_3 generations.

Vogel and Holton (257) report that Oro and Turkey-Florence (C.I. 10080) are highly resistant to other known races of *Tilletia tritici* and *T. levis* but very susceptible to races L–8 and T–11, respectively, and that both are slightly susceptible to T–8. The reaction of the F_3 progenies of Oro crossed with Turkey-Florence showed that the factors for resistance to all three races of bunt apparently have been combined in some progenies and those for susceptibility in other progenies. Some selections from one progeny, 1098, were highly resistant to all three races of bunt as well as to a composite of other races in the F_4 and to 19 individual races in the F_5.

In a Hussar × Hohenheimer cross, Holton and Suneson (125) obtained lines which are resistant to all bunt races so far found in the field, and they are among the very few lines possessing this characteristic so far available.

Covered smut of barley. Relatively little work has been reported concerning breeding of improved varieties of barley resistant to covered smut. Two reasons may account for lack of these inves-

tigations, development of seed treatment measures for control of disease, and lack of satisfactory inoculation technique for obtaining successful infections.

Several investigators, including Briggs (25) and Johnston (139), have reported increased infection of smut by dehulling the seed, and Aamodt and Johnston (4) found that only the embryo had to be exposed to obtain high infection percentages. Tapke (244) describes a method which approaches the simplicity of dusting seed with spores and the effectiveness of inoculating dehulled seed with dry spores. It is often impractical to dehull the seed, or treat the seed as suggested by Tapke (244), especially where large populations are to be considered.

Johnston (139) found in a cross of Glabron (C.I. 4577) × Trebi (C.I. 936) that segregation for reaction to covered smut was not sufficiently clear to establish the mode of inheritance.

Covered smut and loose smuts of oats. Smut of oats differs from that of wheat and barley in that it is difficult to distinguish loose and covered smuts, since the loose and covered condition overlaps, depending on the race of the fungus and the variety of the host. The two oat smut species, *Ustilago avenae* and *U. levis,* have been studied separately and together in many cases. Wakabayashi (259) reported on the reaction of smut of oats and found resistance to be dominant and the reaction to be controlled by multiple factors in a Red Rustproof (C.I. 1815) × Black Tartarian cross. Barney (15) concluded that resistance was determined by one, two or three factors. Gaines (87), in a study of crosses between Red Rustproof and Black Tartarian, Abundance (C.I. 2038), Large-Hulless and Chinese Hulless (C.I. 1003), reported that Red Rustproof had three dominant factors for resistance. Reed (190, 191) found resistance to smut dominant and dependent on a single factor basis on crosses of Black Mesdag (C.I. 1877) × Hulless and Black Mesdag × Silvermine (C.I. 1013). Gaines (88) concluded that the smut-resistant Markton probably contained three factors for smut resistance. Black Mesdag was resistant to both loose and covered smuts, and Hulless was susceptible to both.

In various crosses of Black Mesdag (resistant to both loose and covered smut) with susceptible varieties, Garber *et al.* (92, 93) concluded that resistance was inherited on a single genetic factor basis, resistance being dominant. They (93) found at least one

modifying factor which resulted in transgressive segregation for susceptibility. Hayes *et al.* (112), in crosses of Black Mesdag with homozygous strains from the cross Minota (C.I. 1285) × White Russian (C.I. 531), state that "immunity to smut is dominant to susceptibility". They were unable to determine the genetic constitution of their material for smut reaction, although they suggested the results could be explained by two complementary factors.

Welsh (265) studied the cross of Victory (C.I. 2020) × (Minota-White Russian × Black Mesdag) and found evidence of transgressive segregation in families inoculated with both smuts. Their results indicate that at least two factors govern the inheritance of smut reaction in this cross.

Johnson (129), working with a Black Mesdag × Victory cross, concluded that a two-factor difference existed between the parents, the factors in Black Mesdag being dominant.

Gaines (88) concluded that the smut-resistant Markton probably contains three factors for smut resistance. Coffman *et al.* (62) crossed Markton with nine varieties and were unable to confirm the existence of three factors for resistance to the *Ustilago levis* strains used. There was such a complete gradation of smut percentages within the F_3 lines that it seemed impracticable to divide these progenies into genetic classes on a basis of percentage infections.

Markton was crossed with Black Mesdag (237) and the hybrid progenies inoculated with *Ustilago avenae.* No smutty plants developed in the parents, but infection developed in the F_3 progenies. It appears that the parent varieties carried complementary factors for susceptibility, which were brought together through hybridization.

Austin and Robertson (13) studied a Markton (resistant) × Colorado 37 (C.I. 1640) (susceptible) cross and concluded from the segregation of the smut reaction in the F_3 that a two-factor difference existed between the two parents, and that Markton possessed two dominant factors for resistance. Later they concluded that there was a three-factor difference between the two parents. Reed and Stanton (196) studied crosses of Markton (resistant to both smuts) with five other parental varieties with three types of smut reaction: (*a*) varieties susceptible to both smuts, (*b*) a variety susceptible to the loose smut and resistant to the covered smut, (*c*) a

variety resistant to the loose smut and susceptible to the covered smut. In groups (*a*) there were four crosses, namely, Canadian × Markton, Early Champion (C.I. 1886) × Markton and its reciprocal, and Victory × Markton. Separate series of F_2 plants of these crosses were inoculated with *Ustilago avenae*-Missouri and *U. levis*-Missouri, respectively. Higher percentages of infection were obtained in the series inoculated with covered smut than with loose smut. In the F_3 the progenies reacted to the smuts in a manner entirely independent of each other. Data from both F_2 and F_3 generations suggested a two-factor difference for the loose smut and a single-factor difference for the covered smut. There was a lack of fully susceptible progenies in both series.

In the second group, 17% of the F_2 plants were infected when inoculated with *Ustilago avenae,* and about 75% of the F_3 progenies descended from uninoculated F_2 plants contained smutted individuals. No fully susceptible F_3 progenies were found. The indications were that a single factor pair controlled the reaction to loose smut. Although both varieties were highly resistant to covered smut, 5.6% of the F_2 plants and a small number of F_3 progenies contained smutted plants. They explain this reaction to covered smut on the basis of three factors, one from one parent and two from the other.

In the third group, the reaction of the F_2 plants and F_3 progenies of the hybrid (Monarch × Markton) indicated a single factor difference for covered smut, although there was a noticeable lack of susceptible F_3 progenies. Although the parents were resistant to loose smut, a few F_2 plants were infected and some smutted plants occurred in several of the F_3 progenies.

Schattenberg (207) studied hybrids of Markton crossed with three other varieties. Two distinct strains of loose smut were used, one giving a weak infection on the susceptible parent, the other a more severe reaction. The data on the F_3 progenies which were inoculated with the weak strain of smut indicated a three-factor difference, while no clearly defined behavior was obtained with the other strain of smut. There was a shortage of susceptible progenies, with a slight excess of resistant ones where the weak strain of smut was used.

Reed and Stanton (196) point out that all investigators of crosses involving Markton have found a great preponderance of resistant

F_3 progenies and a corresponding lack of susceptible ones. In a very few cases the results might be accounted for on the basis of a single-factor difference; in others at least two or three independent factors are involved. They mention that in Markton, and in many F_3 plants from crosses on Markton, a blasted condition was observed, that apparently much of this blasting was due to the smut organism in the tissue of the plant. On the basis of this observed reaction, there perhaps might have been expected a larger proportion of fully infected plants in the various hybrid generations. Evidently there is some factor or factors that prevent full expression of susceptibility in hybrids involving Markton. Black Mesdag, a variety very resistant to the races of loose and covered smut used by Reed and Stanton (196), when crossed with susceptible varieties by Reed (192), Stanton *et al.* (237) and Reed (193), showed resistance to be dominant and that segregation occurred on a 3:1 basis. Reed (192) found a parallelism in inheritance of resistance to both smuts in various F_3 progenies. The results indicate that the same factor or closely linked factors were responsible for the resistance and susceptibility in these hybrids.

Hayes *et al.* (113) found Bond and two selections from White Russian Minota × Black Mesdag, designated as Double Crosses A and B, to be resistant to smut in the field. Where Bond was crossed with Double Cross A, some susceptible lines were obtained in F_3, showing that the factors which conditioned resistance were unlike in the two parents. In the crosses of Bond with Iogold (C.I. 2329) and Anthony (C.I. 2143) there were indications of a single major factor difference, although there was some evidence of modifying factors. Previous studies indicated that at least two major factors were necessary to explain the resistance of the Black Mesdag type, the type of resistance exhibited in the double crosses used in these studies. These factors are not allelic to the factor for resistance carried by Bond.

Reed (194) studied the reaction of a large number of varieties and strains to 29 physiologic races of *Ustilago avenae* and 14 of *U. levis*. Under favorable conditions Red Rustproof, used in the early breeding work, had 45% to 60% of smut. Black Mesdag, another variety used in crossing, was resistant to all races of *U. avenae* and to two races, 10 and 14, of *U. levis*. *Avenae barbata* was susceptible to all races. Markton, Navarro (C.I. 966) and

Victoria showed marked resistance to all races of both loose and covered smuts.

Loose smut of wheat. Wheat varieties show a wide range in their reaction to loose smut. Durum wheats, as a group, show more resistance than most of *vulgare* wheats. Club wheats, on the other hand, are relatively susceptible.

Resistance was recessive and dependent upon a single pair of factors in some crosses (99, 184, 200). In another cross of the susceptible variety, San Martin, with the resistant selection, 38 M.A., resistance of the 38 M.A. parent appeared (202) controlled by three recessive factors. Kilduff (141) was not able to give a genetic hypothesis for the inheritance of loose smut reaction in crosses studied by him.

On the other hand, Tingey and Tolman (251) found in crosses studied that three genetic factor pairs controlled the reaction to loose smut. Hope was immune to the inoculum used and carried all three factors. The other resistant parents used in the crosses lacked one or two of the factors and consequently gave progenies of greater susceptibility than in crosses where Hope was one of the parents.

Loose smut of barley. Resistant varieties have been reported, but most of them develop small percentages of smutted plants under environmental conditions favorable for infection. No inheritance studies with loose smut have been reported in the United States, probably because of difficulty in obtaining an epidemic. Nahmmacher (167) and Roemer (200) worked with winter and summer barley varieties and reported that only a single factor pair determined the reaction of the plants. They were not able to obtain highly resistant progenies from moderately susceptible × very susceptible lines, very susceptible × very susceptible, or resistant × moderately susceptible.

Scab of wheat and barley. Arthur (10) was the first of several investigators (11, 48, 107, 127, 150, 208, 209, 222) to report differences in varietal susceptibility to this disease.

Christensen *et al.* (49) reported that common wheats were more resistant than durums, although some of the latter were very susceptible. In two crosses studied, they found most of the hybrids intermediate in reaction to scab, although some lines were as resistant as the resistant parent. All from the Kota × Marquis crosses were susceptible. There are no highly resistant varieties; there-

fore, little work has been done by hybridizing for the purpose of obtaining new resistant varieties.

There are no varieties of barley highly resistant to scab, although there is relative difference in their resistance and susceptibility. The commercial varieties grown in areas where scab is prevalent are very susceptible to the disease. Peatland, selected at the Minnesota station, is the only commercially grown barley which is moderately resistant to scab. Dickson (68) reported Chevron, C.I. 1613 and C.I. 2492 as the most scab-resistant six-rowed varieties, and Svansota (C.I. 1907) a two-rowed variety, that have been found to date. These varieties, especially Chevron and Peatland, are being used in breeding for scab resistance (Shands, 210).

Powdery mildew of barley. Biffen (19, 20) studied the inheritance of reaction to mildew in a cross between *Hordeum spontaneum* (resistant) and *H. hexasticofurcatum* (susceptible). Susceptibility was dominant, and in a small F_2 population of 79 plants he concluded that the data suggested the operation of a single recessive factor for resistance to mildew.

Dietz and Murphy (74) and Dietz (72) studied the inheritance of resistance to mildew in crosses between a resistant variety, Goldfoil (C.I. 928), and four susceptible varieties and obtained a ratio of 3 susceptible to 1 resistant, except in one cross. Goldfoil barley was found (151) to be resistant to four of five physiologic races of barley mildew. Tidd (249) found it resistant to his race 6 but susceptible to race 7.

Mains and Martini (154) tested the same group of barleys to mildew as were tested in a study of leaf rust reaction. A number of varieties were resistant to three races of powdery mildew. A few varieties carried resistance to one or more physiologic races of leaf rust and to one or more of the physiologic races of mildew. Bolivia (C.I. 1257), Sulu (C.I. 1022) and Weider (C.I. 1021) showed marked resistance to all physiologic races of leaf rust and powdery mildew studied.

Stanford and Briggs (230) summarized studies of inheritance to mildew carried on at the California Agricultural Experiment Station. Ten resistant varieties were crossed with one another and with Atlas (C.I. 4118), a susceptible variety, and the genetics of their reaction determined. They found seven different factors for mildew resistance, six dominant and one recessive, the largest num-

ber yet determined for a single disease in any one species of plant. The number of factors in a single variety varies from one to three. The Algerian (C.I. 1179) and Kwan (C.I. 1016) factors (35) were found to be linked; the remaining five appear to be independent. Tidd (250), using race 6, found a single factor for resistance to mildew in a cross between resistant Nepal 595 and susceptible Featherstone (C.I. 1120). This factor must differ from any of the seven reported above because Nepal is completely susceptible to race 3.

Flax wilt. The disease caused by *Fusarium lini* is characterized by a wilting of flax plants at any stage from emergence of the seedling to maturity. The amount of wilt in susceptible strains has been shown by Tisdale (254) and Jones and Tisdale (140) to vary with temperature. Below 60° F. wilt-susceptible varieties escaped injury from wilt. Bolley (21), on the basis of preliminary observations, concluded that by growing any good variety of flax on wilt-infested soil and selecting resistant plants, resistance could be built up through association of the plant with the disease organism. Robinson (198) explained this condition as an elimination of non-resistant genotypes in lines heterozygous for resistance.

According to Barker (14), varieties selected as resistant to wilt do not lose their resistance, whether grown on clean or wilt-infested soil. A variety may become susceptible to the extent of the admixtures in it. Moreover, since growth of the wilt organism depends on environmental conditions, temperature and other climatic conditions determine the degree of resistance (36).

In crosses between wilt-resistant and susceptible strains, the F_1 is in general intermediate, although in certain crosses resistance or susceptibility may be dominant (8, 41, 254). Types of segregation obtained in F_2 and later generations indicate that several factors are involved in the inheritance of reaction to wilt. The number of factors conditioning resistance is difficult to determine because resistance is relative and is influenced greatly by environmental factors.

Burnham (41) found that selected lines bred true for different degrees of wilt resistance and concluded that wilting in pure-line resistant strains was not due to genetic segregation. In F_3 some of the lines were as resistant as the resistant parent.

Allison and Christensen (8) found that when Bison (C.I. 389),

a highly resistant variety, was used as a parent, the percentage of resistant segregates obtained was usually higher than when other varieties, almost equally resistant, were used. Some of the F_4 and F_5 progenies of the crosses between Bison (wilt-resistant but susceptible to rust) and Newland (wilt-susceptible but immune to rust) were resistant to both wilt and rust and maintained the desirable agronomic characters of the parents.

Varieties may become less resistant to wilt after a few years or if grown in a different locality. This may be due to physiologic specialization of the organism, since Broadfoot (36) identified a number of races from a wide area. There are some varieties, such as Bison, Buda (C.I. 326) and Argentine, which are resistant to wilt over a wide area (75).

Root rots. This group comprises a large number of facultative parasites which are widely distributed, live in the soil, attack a large group of hosts and thrive under a wide range of conditions. In general, any condition unfavorable for growth of the host favors development of root rot diseases. Weak, slow-growing plants, low in vigor, are more susceptible than thrifty, vigorous ones. Root rot organisms can attack the plants any time during their development (37, 44, 118, 157). The most common root diseases of small grains are: Take-all, *Ophiobolus graminis* Sacc.; foot and root rots, *Helminthosporium sativum,* P. K. and B. and other species of *Helminthosporium, Fusarium* and *Pythium; Cercosporella herpotrichoides,* Fron.; *Rhizoctonia,* spp.; *Leoptosphaeria* spp.; and *Wojnowicia* spp.

In the United States, take-all is most important in the winter wheat areas; *Helminthosporium, Fusarium* and *Pythium* in the spring wheat areas (44, 121); and *Cercosporella* foot rot in the Columbia Basin of the Pacific Northwest (215, 218).

The various root rots attack many wild and cultivated grasses in addition to the cereals (44, 142, 143, 176, 203, 204, 216, 218). *Ophiobolus graminis* readily attacks wheat and barley but does not attack oats (44, 176, 203). Wheat and barley are susceptible to *Cercosporella herpotrichoides,* and oats are nearly immune under artificial inoculation (218). All cereals are susceptible in early stages of development to *Rhizoctonia solani* (204).

Sanford and Broadfoot (205) have shown that the natural microflora of soil has a marked inhibitive effect on development of cereal

root-rotting fungi. Their results seem to offer a partial explanation of the frequent failures to obtain successful infections where inoculum has been added to the soil. Each of the root disease fungi, which have been extensively studied, has been found to include from several to many distinct races which differ in temperature relations and pathogenicity (66, 118, 203, 215, 217).

There are few if any commercial varieties of wheat or barley highly resistant to root diseases under all conditions. Use of adapted varieties and of varieties less susceptible to this type of injury have helped in reducing losses (68).

Inheritance of the reaction to these various root rots has not been studied extensively. With *Helminthosporium sativum,* spot blotch of barley, Hayes *et al.* (115) found resistance and susceptibility to be inherited characters, although dependent on more than a single factor. Griffee (100), in a cross of Svanhals (C.I. 187) × Lion (C.I. 923), concluded that at least three factors were concerned in the production of resistance of the type of Svanhals. One factor was linked with the two-row factor, one with the factor for rough awns, and one with the factor for white glumes.

ACCOMPLISHMENTS

The above brief review indicates that much progress has been made in breeding varieties of wheat, oats, barley and flax for resistance to various diseases. Success in breeding for disease resistance, however, means producing varieties that not only are resistant to disease but also are satisfactory in other respects. It seems desirable, however, to state briefly to what extent breeding for resistance to diseases has resulted in new varieties of commercial importance. Only a few of the outstanding accomplishments will be mentioned and most of these have been done through the cooperative effort of the United States Department of Agriculture and the states mentioned.

One of the outstanding accomplishments of small grain breeding in the United States is the production of varieties of wheat resistant to stem rust. Previous to 1904 there were sporadic outbreaks of this disease, but it was not a major factor in production. In 1904 and again in 1916 damage was severe and widespread, amounting in each year to not less than one-hundred million bushels of grain in the United States alone. Since 1916 severe losses occurred in

1919, 1920, 1921, 1923, 1927, 1935 and 1937 with measurable losses in practically all other years. As a result of experiments at the South Dakota and North Dakota Agricultural Experiment stations in the early years of the century in cooperation with the United States Department of Agriculture, the outstanding resistance of certain varieties of emmers and durum wheats was established (43). Attempts were immediately made to transfer this resistance to common wheats, but these early efforts were generally unsuccessful because of sterility in the hybrids as a result of the unbalanced chromosomal complex and because of linkage between rust resistance and certain undesirable characters in the durum and emmer parents.

Similar cooperative experiments were undertaken at the Minnesota Agricultural Experiment Station about 1905 where somewhat later the first successful transfer of stem rust resistance of durum wheat to common wheat was made. The first commercial variety of wheat common highly resistant to rust to be grown commercially—Marquillo—was produced as a result of this early work, the parents being Marquis and Iumillo durum. Marquillo proved to be highly resistant to stem rust and possesses most of the highly desirable characters of its *vulgare* parent but proved unsatisfactory because of too much yellow pigment in the flour and has never been grown extensively.

A sister selection of Marquillo, resistant to a collection of physiologic races in the field, was crossed with a Kanred × Marquis selection which was immune to 11 physiologic races of stem rust in the seedling stage. The cross was made in 1921. From this cross, Thatcher was produced and released to farmers in 1934 (111). Under field conditions Thatcher has been rather highly resistant to stem rust, although under artificially induced epidemic conditions, where many races of rust are used, it has varied seasonally from moderately to highly resistant. It is high yielding, early maturing, stiff strawed, and has high milling and baking qualities. It is susceptible to leaf rust and scab. Because of its stem-rust resistance, it is now the widely grown spring wheat, being grown on about 17 million acres in the United States and Canada.

Ceres is a selection from Kota (a resistant hard red spring wheat) crossed with Marquis (260). The cross was made in 1918 and the variety released by the North Dakota Agricultural Experiment

Station for commercial growing in 1927. This variety, resistant to stem rust at the time it was released, although its rust reaction under artificially induced epidemic conditions has varied seasonally from high resistance to near susceptibility, was early maturing and of high quality. It was widely grown until the severe rust epidemic of 1935 when it was severely injured by stem rust, and has now been replaced by rust-resistant varieties wherever rust epidemics are likely to occur.

Hope (C.I. 8178) and H–44 were developed from a cross between Yaroslav emmer and Marquis wheat by McFadden (155). These new varieties are resistant to leaf and stem rusts and loose and covered smuts, but are susceptible to black chaff. Hope was released to farmers in 1926, but has rather weak straw, low yield and a grayish colored flour. Its main value has been for breeding purposes because of its high rust resistance. H–44 was not released for commercial production. Like Hope, H–44 has been used extensively in breeding work of its high resistance to rusts. Most of the material now being tested, particularly in the spring wheat area, has been derived from a cross having either Hope or H–44 as one of the parents. Four varieties have been produced from these crosses in which resistance to leaf and stem rusts and bunt have been combined with other desirable agronomic characters and quality.

Hope was crossed with Ceres in 1926, and from this cross Pilot (C.I. 11428) was developed by Clark (54). Pilot is resistant to stem rust and bunt and moderately resistant to leaf rust, is a high-yielding wheat and of good milling and baking quality. Pilot has weak straw. It was released for commercial growing in 1938. Another variety, Rival (C.I. 11708), released the same year, has a stronger straw than Pilot and was produced from a Ceres × (Hope-Florence) cross made in 1926 (239). Rival has a tendency to shatter under certain conditions. It possesses about the same characteristics as Pilot, and, in addition, is resistant to loose smut. Both Pilot and Rival were released by the North Dakota Agricultural Experiment Station and are grown in North and South Dakota and western Minnesota. It was estimated that 500,000 acres of these wheats were grown in 1941, and this acreage will increase because of their greater resistance to leaf rust and the serious damage to Thatcher in this year from this disease.

Two other spring wheats, Renown (C.I. 11947) and Regent (C.I. 11867), which were developed from a H–44 × Reward cross (170) in 1926, were released by the Dominion Department of Agriculture for commercial growing in 1939. Renown has proved highly resistant to leaf and stem rusts and stinking smut, and moderately resistant to loose smut. Regent is a high-yielding variety, medium early in maturity, and is resistant to leaf and stem rusts and bunt. These wheats are recommended for growing in Manitoba and eastern Saskatchewan where leaf and stem rusts may cause injury.

Wabash (C.I. 11384) is a selection from a natural hybrid of Fultz and an unknown variety. It was selected in 1924 and released by the Indiana Agricultural Experiment Station to farmers of Indiana and Illinois in 1938. It is superior to standard soft red wheats in yield, winter-hardiness and resistance to leaf rust and mosaic (Clark, 55).

Bunt is a serious disease in the United States, particularly in the Pacific Northwest. From the early breeding work begun by Gaines in 1915, Ridit (C.I. 6703) was developed from a cross of Turkey × Florence and released by the Washington Agricultural Experiment Station in 1923 (85). It is resistant to bunt and shattering, with high-yielding ability and good milling and baking qualities. Later, Albit (C.I. 8275), the result of Hybrid 128 (C.I. 4512) crossed with White Odessa (C.I. 4655), was released for commercial growing in 1926. The superior characters of this variety at the time of its release were smut resistance, winter hardiness and good yielding ability (206).

Gaines and Schafer (89) report that Albit increased in acreage rapidly until 1935 when the season was unfavorable for it. New races of smut that attack it had become common in some sections so that it did not appear to be as resistant to smut as in former years. For that reason many farmers changed to some other variety. Hymar (C.I. 11605), released in 1935, was produced from a cross made in 1922 of Hybrid 128 with Martin. Hymar is resistant to one physiologic race of smut to which Albit is susceptible.

Oro is a smut-resistant selection of Turkey released by the Sherman County Branch Station, Moro, Oregon, in 1927. This variety is adapted to certain sections in Oregon and Washington (59).

Another variety, Rex (C.I. 10065), developed from a cross between White Odessa and Hard Federation in 1921 (52), was released by the Sherman County Branch Station, Moro, Oregon, to the farmers in 1933. This variety is a soft winter wheat which yields well, is early maturing and resistant to lodging, shattering and bunt. This is now the most widely grown variety in the Pacific Northwest.

Relief (C.I. 10082) was produced from a cross of Hussar × Turkey in 1925 (252) and released by the Utah Agricultural Experiment Station for commercial growing in 1931. It is a hard red winter wheat, resistant to several physiologic races of bunt, especially the dwarf bunt to which very few varieties are resistant. Relief is grown chiefly in Utah and southern Idaho.

Gaines and Schafer (90) point out that the use of smut-resistant varieties and improved seed treatment has resulted in a steady decline in losses from bunt. The number of cars of wheat grading smutty at the Pacific Coast Terminals has decreased from about 50% to 5% during the years 1931 to 1939, inclusive.

Briggs (34) reports the production of bunt-resistant wheats by the backcross method, by crossing Martin (resistant) with Baart (C.I. 1697) and several other varieties. Bunt-resistant Baart-like selections were crossed with Hope (resistant to rust) and backcrossed to Baart selections. From this series of backcrosses lines have been selected which are resistant to bunt and stem rust, and appear to have most of the other Baart characters. In another series of backcrosses, Briggs has selected backcrossed lines which are bunt-, hessian fly- and rust-resistant, yet have many of the other characters of the original Big Club parent (C.I. 4257).

In the early oat breeding work most of the new varieties were improved strains from standard varieties selected because of their resistance to certain diseases and having otherwise desirable agronomic characters, Richland and Iogold, two varieties with outstanding characters, are stem rust-resistant selections made from the Kherson variety in 1906 (39, 40). These varieties were distributed by the Iowa Agricultural Experiment Station. Rainbow is a pure line selection from the Green Russian (C.I. 2342) variety which was selected for its stem-rust resistance (235). This variety was released by the North Dakota Agricultural Experiment Station and is adapted to this State and northwestern Minnesota because of its high stem-rust resistance.

Fultex (C.I. 3531) was selected from a cross (No. 3020) between Fulghum and Victoria and was released by the Texas Agricultural Experiment Station in 1940. This variety is resistant to smut and crown rust (234).

The Wisconsin Agricultural Experiment Station released the variety Vicland (C.I. 3611) for growing in Wisconsin in 1941. It was developed from a cross (No. X S 1098) between Victoria and Richland. The leaves of Vicland fleck when atacked by crown rust, and it is susceptible only to stem rust races that now occur late in the season. It is resistant to smuts (234).

Two other varieties, Ranger (C.I. 3417) and Rustler (C.I. 3754), have been developed from a cross (No. X 3012) between Nortex (C.I. 2382) and Victoria. The superior characters of these new red oat varieties are earliness, high yield and resistance to the races of crown rust and smut that occur in Texas. These varieties were to be released by the Texas Agricultural Experiment Station in the fall of 1941, and are recommended for certain sections in this state (234).

Huron (C.I. 3656) is a selection from a cross between the Markton and Victory varieties. The superior characters of this variety are high yield and test weight and resistance to smut. This variety was released in 1940 by the Michigan Agricultural Experiment Station for growing on soils in the lower peninsula of that state (76).

Uton (C.I. 3141) was originated from a cross between Markton and Swedish Select (C.I. 134). It is high yielding and resistant to the races of smut prevalent in Utah and adjacent States. The variety was distributed by the Utah Agricultural Experiment Station in 1937 (253).

The outstanding variety for smut resistance is Markton which originated from an unnamed oat (C.I. No. 357) made in 1911. The superior characters of this oat at the time of its release were early maturity, high yield, resistance to smut, thin hull and excellent quality (238). Markton has been used as a smut-resistant parent to cross with Fulghum, and from this cross Fulton was developed by the Kansas Agricultural Experiment Station and released in 1939. Fulton combines smut resistance with early maturity, high yield and quality (232). Carleton (C.I. 2378) was developed from a selection of Sixty Day crossed with Markton, made in 1921 (232). This variety has resistance to nearly all the races of smut and to

Fusarium culmorum. It was distributed to farmers by the Sherman Branch Experiment Station, Moro, Oregon, in 1937 and 1938 for growing in the dry-farming areas. Both Fulton and Carlton are susceptible to the rusts of oats. Bannock (C.I. 2592) originated from a cross of Markton with Victory, made in 1923. It is superior in having smut resistance, high yield and quality, and has white kernels (232). It was distributed by the Idaho Agricultural Experiment Station for growing in southern Idaho.

The two varieties, Hancock (C.I. 3346) and Marion (C.I. 3247), are selections from Markton crossed with Rainbow in 1928 (233). It has been possible to combine in these new varieties the smut resistance of the Markton parent and resistance to some of the physiologic races of crown and stem rusts from the Rainbow parent. In addition, these new varieties are early maturing, of good quality and exceptionally stiff strawed.

Boone (C.I. 3305) is a selection from a cross (No. × S 1098) of Victoria and Richland made in 1930. The superior characters of this variety are early maturity, high yield, quality and high resistance to a number of physiologic races of stem rust, crown rust and the smuts of oats (233). Marion, Hancock and Boone were released by the Iowa Agricultural Experiment Station for commercial growing in Iowa in 1940. More recently, Bond, a variety highly resistant to crown rust, has been used in the oat improvement program by crossing it with desirable commercially grown varieties having resistance to stem rust and smut. A number of selections combining the high resistance to crown and stem rusts and smuts in the field and other desirable agronomic characters are being widely tested (108, 164).

One new variety of barley, Velvon, has been developed from Colorado selection 3063 crossed with Trebi (268). This variety is smooth awned and resistant to covered and loose smuts under the conditions in Utah where it was developed.

Chevron and Peatland are being used extensively in the barley breeding program because of their resistance to stem rust and moderate resistance to scab. These varieties have rough awns and have been crossed with desirable smooth awned varieties such as Velvet and Barbless. No new varieties noted for resistance to disease, particularly scab and foot rot, have been released recently. One of the chief difficulties in breeding for resistance to these diseases is the lack of highly resistant varieties which may be used as parents.

Varieties resistant to one of the two important diseases, rust or wilt, are now available. Bison and Redwing (C.I. 3201), two of the most widely grown varieties, are resistant to wilt. Much of the breeding work, therefore, is directed toward combining in a single variety, wilt and rust immunity with high yield and high percentage of oil having superior drying qualities. Some progress has been made and more may be expected in the future. A summary of available flax varieties and their superior characters is given by Dillman (75).

The present accomplishments justify the belief that new varieties having progressively higher qualities and greater disease resistance will be produced in the future.

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Articles in course of preparation

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